AMERICAN MUSEUM
Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N.Y. 10024
Number 3204, 11 pp., 4 figures August 29, 1997

A Fossil Mantis (Insecta: Mantodea) in Cretaceous Amber of New Jersey, with Comments on the Early History of the Dictyoptera*

DAVID GRIMALDI[1]

ABSTRACT

The nymph of a new genus and species of mantis, *Jersimantis luzzii,* is described, in amber from the mid-Cretaceous (Turonian) of central New Jersey. It is the oldest mantis from North America and only the second report for Mesozoic mantises. Although it cannot be definitively placed into a modern family, it is plesiomorphic compared to most modern mantises in the head and pronotal shape, and structure of the raptorial forelegs, similar to what is found in the most primitive extant family of mantises, the Chaeteessidae. The age and apparent phylogenetic position of *Jersimantis* are consistent with the view of a late Mesozoic radiation of the Dictyoptera, not a Paleozoic radiation as has sometimes been suggested. It is hypothesized that the Isoptera and Mantodea are closely related to the "ovipositorless" roaches that first appear in the early Cretaceous/late Jurassic (into the present) and that the Mesozoic and Paleozoic roaches with ovipositors represent a paraphyletic assemblage.

INTRODUCTION

Among the most recognizable insects are the ones belonging to the Dictyoptera: the cockroaches, termites, and mantises. The eusocial termites often live in very large colonies and digest cellulose with bacterial and protozoan gut symbionts; the mantises are famous for their predatory habits and morphology. When compared to the rather gen-

* Paleontology of New Jersey amber, Part V.

[1] Chairman and Curator, Department of Entomology, American Museum of Natural History.

Copyright © American Museum of Natural History 1997

ISSN 0003-0082 / Price $1.60

eralized roaches, it strikes even many entomologists as peculiar that these orders are closely related. Nonetheless, synapomorphic features of the male genitalia, wing venation, and head structure indicate that the Dictyoptera is almost unquestionably monophyletic (reviewed in Hennig, 1981). As I discuss below, the monophyly of the Blattodea (living and extinct roaches) is seriously questionable (but see Jarzembowski, 1994). The monophyly of the Mantodea is unquestionable. Besides some features of the wing, all of the diagnostic apomorphies of mantises are associated with predation: large raptorial forelegs (having a large, mobile coxa, and crassate femur with 2 rows of spines, and an opposing tibia with apical spurs), a head that is freely mobile and with large eyes for an improved frontal field and binocularity. With the exception of the most primitive family of mantises, the Chaeteessidae (with extant and fossil species), virtually all mantises have an elongate prothorax, no doubt an adaptation for extending the reach of the raptorial forelegs.

As will be discussed below, the fossil record of the Dictyoptera is perplexing. Although termites and mantises have very incomplete records, particularly for the Mesozoic, and roaches have an excellent fossil record, the history of the roaches is ancient—extending to the upper Carboniferous—while the history of the termites and mantises is seemingly much younger. To some extent this might just reflect disparity in the records, but when the systematic positions of the fossils are considered, the disparity between roaches and other dictyopterans is, in fact, accentuated. To help fill the huge gap in the Mesozoic history of the mantises, a report is made on a newly discovered specimen in Cretaceous amber from New Jersey, U.S.A.

Materials and Methods

The specimen was found among hundreds of pounds of amber extracted from two excavation sites in lignitic strata from the Cretaceous of central New Jersey (exact location on file in the Entomology Dept., AMNH, to be published later along with stratigraphy). The location corresponds closest to site number 5 in Grimaldi et al. (1989), described as Cenomanian. Site 5 and this site both lie just above the South Amboy Fire Clay, marking the Raritan Formation. Recent palynological evidence indicates the present site to be Turonian (90–94 Ma). Crude amber was washed, tumbled in a series of three sizes of grits, then screened for inclusions. Pieces with inclusions were embedded in a polyester casting resin under vacuum (to impregnate the cracks), and then trimmed with a water-fed diamond saw, ground with water on lapidary wheel using 320 and 600 grit paper, and polished. The embedding allowed optimal viewing of the inclusion, without having the amber, which is very brittle, fracture. A paper giving a detailed description will be published later. A Zeiss SV-8 and Leitz stereoscope were used for morphological examination.

Acknowledgments

This and hopefully many other papers to come on the fossils in New Jersey and other Cretaceous ambers are the product of a dedicated group of people. First, I owe deep thanks to the intrepid collectors who spent weeks of hard labor digging up amber in central New Jersey. Probably the most inspired collector was Keith Luzzi, discoverer of the specimen featured in this paper. The species patronym is a small honor indeed for such dedication. Secondly, the study of this fragile amber was made possible by innovations developed by Henry Silverstein ("Hank") in my lab at the AMNH, and by Paul Nascimbene ("Nash"). Hank has been personally very generous to the research, and Nash's keen eye has found many a rare inclusion during his screening of crude amber. Lastly, equipment, wages, and ambitious machine excavations have been made possible through funding by Henry Walter, trustee of the AMNH. Although I chose not to adopt all suggestions, thorough review of the manuscript by André Nel (Paris), Andrew Ross (London), and Ted Pike (Calgary) were extremely helpful. To all I am grateful.

DICTYOPTERAN PHYLOGENY

A critical phylogeny of any group is essential for accurate interpretation of fossils. Fortunately for studies on the Dictyoptera,

during the past five years there has been a plethora of rigorous phylogenetic work on this group of orders, both morphological and molecular.

The first studies to carefully consider dictyopteran characters in a phylogenetic context are those of Boudreaux (1979) and Hennig (1969, 1981). (The latter author also referred to the Dictyoptera as the "Blattopteroidea," as did Grassé [1949].) Given the almost unquestionable monophyly of the Dictyoptera (Kristensen, 1975, listed six synapomorphies alone), there are four possible sets of relationships, but one has very strong support. Boudreaux's (1979) scheme has Blattaria and Mantodea as sister groups; Hennig proposed Blattaria and Isoptera as sister groups. Kristensen (1975) left the three orders unresolved. Later, three studies addressed the problem further. Thorne and Carpenter (1992) is the most comprehensive analysis yet, being based on 70 behavioral, developmental, and morphological characters principally drawn from previous studies. Their phylogeny supports that of Boudreaux (1979). However, Kristensen (1995) changed five of the characters in the data matrix of Thorne and Carpenter (1992): one was replaced with a different character, the other four had their polarities reversed. Using the same algorithm for analysis, this slightly altered matrix yielded a slightly longer tree (111 steps instead of 109), and slightly lower character consistencies (CI = 0.86 instead of 0.88, RI = 0.82 instead of 0.84), but with a completely altered topology: Isoptera and Blattaria become sister groups. Homologies of individual characters are discussed at length elsewhere (and were presented by Kristensen [1995]), but suffice it to say that the Blattaria + Mantodea grouping is highly unstable on the basis of only 7% of the characters in the analysis by Thorne and Carpenter (1992).

There is additional support, however, for Boudreaux's hypothesis of a Blattaria + Mantodea clade, with nucleotide sequences (DeSalle et al., 1992; Kambhampati, 1995). DeSalle et al. analyzed portions of the 18S rDNA gene in a small sample of dictyopterans: a mantis, a roach, and four termites. The intention of that study was not to resolve dictyopteran relationships, but to put the DNA sequences of an extinct termite in Dominican amber into a phylogenetic context; the results nonetheless bear on the question of dictyopteran relationships. The molecular characters in DeSalle et al. (1992) give a unique (indeed, unexpected) hypothesis of an Isoptera + Mantodea sister grouping, with Blattaria in a basal trichotomy with that clade plus a grasshopper. In an analysis combining the molecular characters with the characters from Thorne and Carpenter (1992), a single, most parsimonious cladogram confirms the topology of Boudreaux (DeSalle et al., 1992).

Last, and much more important, is the study by Kambhampati (1995), which has the most comprehensive taxonomic sampling: 3 termites, a mantis, and 32 roaches, using sequences from 16S rRNA and 12S rRNA genes. A single most parsimonious tree resulted from analyses using strict parsimony criteria, and this tree supported the Boudreaux hypothesis of the Blattaria + Mantodea clade. The extensive sampling of roaches in the Kambhampati study is extremely significant, for it addresses concerns about the monophyly of the cockroaches, such as expressed by Kristensen (1989, p. 302): It is "debatable whether cockroaches are themselves monophyletic, or whether they are paraphyletic in terms of termites." Kambhampati's data, analyzed using bootstrap parsimony, actually yielded a basal pentatomy of termites, the mantis, and three roach clades. But, when the data were analyzed using strict parsimony, a tree 162 steps shorter was produced, yielding the Blattaria + Mantodea topology, with a monophyletic Blattaria.

It can be said with some confidence that dictyopteran relationships are a sister grouping of Blattaria + Mantodea, and the sister group to this clade is the Isoptera.

FOSSIL RECORD OF THE DICTYOPTERA

If we take the Blattaria + Mantodea sister grouping as our working hypothesis, and strictly apply sister-group dating to the lineages, should we expect mantises and termites to have a fossil record that extends to the Carboniferous with the first appearance

of roaches? Kukalova-Peck (1991: 166) suggested this to be the case: mantises "probably arose from L. Carboniferous blattoids . . .," to which Balderson (1991: 348) concurred: "the fossil record [of Mantodea], although sparse, is sufficient to indicate a common *Paleozoic* ancestry with the Blattodea." Hennig (1981: 195), too, believed such antiquity was possible for the Mantodea: "we shall probably have to go back at least as far as the Upper Carboniferous to find the common ancestors of the Blattodea and Mantodea, if we consider them to be sister groups." Given a fossil record even as notoriously incomplete as that for the insects, there are still unexplained disparities in the fossil records of these three orders based on sister-group dating.

The fossil record of blattoids is legendary, with primitive roaches first appearing in the fossil record in the upper Carboniferous, and various lineages well represented in the record since then. The record of the Isoptera, however, does not reflect such antiquity. Although the Isoptera have a much sparser fossil record than the roaches, all Mesozoic records are from the Cretaceous and are of the primitive families Hodotermitidae and possibly (based on two records) the Mastotermitidae (Emerson, 1967; Jarzembowski, 1981; Lacasa-Ruiz and Martinez-Delclos, 1986; Krishna, 1990; Grimaldi and Krishna, unpubl.). Nel and Paicheler (1993) placed *Valditermes* Jarzembowski, 1981 from the Wealden Clay in their revised concept of the Termopsidae (the Hodotermitidae being paraphyletic in their view). Despite Krishna's (1990) reinterpretation of the venation of *Valditermes* as indicating a probable mastotermitid, Jarzembowski persists in attributing this fossil to the Hodotermitidae. Another possible mastotermitid, *Mastotermes sarthensis,* is represented by a wing in Cenomanian amber from northwestern France (Schlüter, 1989). (This reference was missed by Thorne and Carpenter [1992], who stated that mastotermitids "do not appear in the fossil record until the Eocene [60 mya—sic]"). Restricted today to a single species in Australia, mastotermitids in the early Tertiary were diverse and nearly global, but Cretaceous mastotermitids are surprisingly few, with Schlüter's and Jarzembowski's specimens two possible examples. Triassic insect nests with no bodies have been reported as termites nests (Hasiotis and Dubiel, 1993, 1995), but such conclusions are equivocal. The Isoptera *clearly* have had no pre-Mesozoic history. André Nel (personal commun. to DG, 1996) mentioned the existence of " 'termite'-like wings in [the] Upper Permian of France." Illustrations of these specimens have not been seen by myself, so it is possible that these are merely highly convergent with the Isoptera, as is known for *Trachopteryx* Carpenter (Permian of Kansas) and several Permian protorthopterans.

Unfortunately, the fossil record of mantises is even sparser than for the Isoptera. Until recently, all were from the Tertiary. Carpenter (1992) cataloged some of the available names, such as the few mantises described from Eocene Baltic amber and Oligocene shales of Florissant, Colorado. Nel and Roy (1996) reviewed and redescribed three Paleocene mantises from Menat, France. Schlee (1990) showed a photo of a mantis nymph in Dominican amber, as did Poinar (1992: 103), who also stated that no descriptions of mantises in the Miocene amber from the Dominican Republic have been published "because only young juveniles have been recovered." Grimaldi (1996: 93) illustrated an alate adult mantis (and a nymph) in Dominican amber and, in fact, at least two adult mantises are known. Dominican amber harbors, no doubt, the most diverse fossil record of the mantises, with several dozen specimens and at least 10 taxa now known. However, given the Miocene age of this amber, most mantises probably belong to living genera as do many other Dominican amber insect groups.

Gratschev and Zherikhin (1994) presented a review of the fossil Mantodea and were the first to describe mantises from the Cretaceous. All of the compression fossil specimens came from the Zaza Formation, Valangian-Hauterivian (lower Cretaceous) of Buryat, Russia; the Undurukha Formation, Barremian-Aptian (lower Cretaceous) of Bayan-Khongor Aymak, Mongolia; and from the Turonian of Kzyl-Orda, Kazakhstan (the last locality contemporaneous with the New Jersey amber site). Most specimens are represented as forewings or fore and hind wings.

The wings possess several venational features synapomorphic for the Mantodea, including a long subcostal vein close to the radius; numerous anal veins terminating freely in the hind margin of the forewing (some Paleozoic roaches also have this feature), and an enlarged jugal lobe of the forewing. The only compression fossilized mantis body they reported was *Cretomantis larvalis,* from the Zaza Formation. It has an apomorphically narrow prothorax and strongly crassate forefemora with strong spines. Two Cretaceous amber fossils were also reported, both from the Kheta Formation, Santonian (upper Cretaceous) of Taymyr, northern Siberia. Both amber fossils are nymphs but show obvious plesiomorphic features. Comparisons to the New Jersey fossil are discussed later.

Since the report by Gratschev and Zherikhin, a mantis has been discovered in Cretaceous amber from Canada (Pike, 1995), although none are known from Lebanese amber (Grimaldi, personal obs.). The present paper is a small contribution that helps fill a huge gap in the Mesozoic record of the Mantodea. Although sparse, the few Cretaceous mantises studied are consistent with a diversification pattern similar to that of the Isoptera.

Reconciling disparities in the fossil record of the Dictyoptera must lie in how we define the roaches. As Thorne and Carpenter (1992) briefly discussed, fossil "roachoids . . . have received a reasonable amount of attention because of one rather dramatic character": an ovipositor. A long, swordlike ovipositor is found in Paleozoic roaches, and the structure gradually decreases in size through time until in the latest Jurassic and early Cretaceous, when most roaches possessed very short ovipositors, or completely internalized, rudimentary ones (as in all modern roaches). Morphology of the fossils (Vishniakova, 1968) reveals that the ovipositor is derived from sternites 8 and 9. Ontogeny of modern roaches (Nel, 1929) reveals that the three pairs of rudimentary, internal ovipositor valves are also derived from sternites 8 and 9 (not from sternite 7 as evidence based solely on adult specimens would indicate). The internal valves in modern roaches function to manipulate eggs in a bursa for the formation of the ootheca, a hardened sac of eggs produced by the great majority of species (the feature is lost in a few groups).

Thus, modern roaches—for which the name Blattaria should be reserved—appear to be a clade that originated in the late Jurassic or early Cretaceous, and are defined by this loss of an external ovipositor. A nagging problem about such a young age are the few reports of apparent roach oothecae from the Carboniferous, which Hennig (1981) discussed at some length and he and others regarded with skepticism. Oothecae could not be produced by roaches with ovipositors, so it is unlikely that Paleozoic oothecae existed unless there were Paleozoic roaches that had lost the external ovipositor (it is uncertain for some specimens if the ovipositor was simply not preserved or if these were males). This problem was first articulated by Laurentiaux (1951). Oothecae apparently exist in the Stephanian of France (A. Nel, personal commun. 1996), but it is unclear if they were produced by roaches or not. Highly vestigial rudiments of the internal valves exist in some termite families and are least atrophied in one of the most primitive termites, *Mastotermes.* Mantodea have very small, external ovipositor valves, which corresponds to their phylogenetic position as the basalmost group of living Dictyoptera.

My hypothesis—modified slightly from Hennig (1969, 1981)—is that Dictyoptera is a monophyletic group comprising the "ovipositorless" roaches and the fossil and extant forms of mantises and termites (fig. 4). This would make the Paleozoic and early Mesozoic roaches a paraphyletic group. The stem-group dictyopteran probably appeared in the Jurassic, perhaps the Triassic. This is the simplest interpretation conforming to the cladogenesis and paleontology of the group. Jarzembowski (1994) debated this view, on the basis of ovipositor reduction and internalization being a "progressive trait" and not unique to the Blattodea. A trait can certainly be a synapomorphy as a step in its progression or transformation, and convergence hardly precludes a trait from being synapomorphic at some level. Interpretations of dictyopteran relationships maintaining that Dictyoptera includes the Paleozoic roaches with ovipositors, that mantises and termites have a Paleozoic origin, and that all three orders

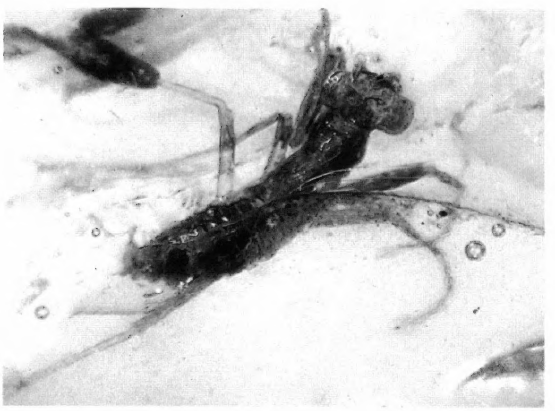

Fig. 1. Photograph of *Jersimantis luzzii,* holotype. Amber piece is embedded in a small block of casting resin, to prevent cracking during preparation and for sealing the amber against atmospheric oxidation.

today have independently lost the external ovipositors, conflict with the observed fossil record, and are not cladistically parsimonious. Presumably, my hypothesis should be supported by the reports of new fossils, for which opportunity is now taken.

SYSTEMATICS

JERSIMANTIS, NEW GENUS

ETYMOLOGY: Derived from the state of the type locality, New Jersey.

DIAGNOSIS: Nymphs with a broad head, width of head about 1.6 times width of pronotum; ocelli apparently absent; pronotum short and nearly square, length and width virtually equal; raptorial forelegs with femur only slightly thicker than other femora, having ventrolateral row of about six fine, stiff, spiculelike bristles; foretibia with pair of ventroapical spurs, the one on mesal corner twice as stout, and two ventrolateral rows of six to eight stiff, fine bristles.

TYPE SPECIES: *Jersimantis luzzii,* n. sp.

Jersimantis luzzii, new species
Figures 1–3

HOLOTYPE: AMNH NJ-425 (KL-479), almost certainly an immature (nymphal) specimen in a transparent dark yellow-orange piece of amber from Sayreville, New Jersey, Raritan Formation (Turonian). Collected by Keith Luzzi, 1996. The amber piece is 6 × 10 mm and was embedded in casting resin, trimmed to a block 11 × 13 mm, which allowed the piece of amber to be trimmed into it, giving a flat, polished view of the inclusion (fig. 1).

ETYMOLOGY: Specific epithet a patronym in honor of Keith Luzzi, the collector of this and many other wonderful New Jersey amber specimens donated to the AMNH.

DESCRIPTION: Body length 3.37 mm from apex of head to abdomen (excluding cerci). **HEAD:** wide, 1.6 times width of pronotum, 1.7 times length of head. Eyes large and bulging, situated entirely laterally, not pushed forward. Vertex broad and rather flat; *ocelli apparently not present.* Broad, v-shaped, shallow ridge present in middle of head. Antennae broken off at bases; flagella lost. Face protrudes beyond anterior margin of eyes. Mouthparts hypognathous, most with a milky coating, except apices of labial and maxillary palps. Labial palps shorter and slightly thinner than maxillary palps, curved strongly mediad, with two segments apparent, the apical segment distinctly tapered. Maxillary palps with three visible segments. **THORAX:** Pronotum short, width × 1.1 times length, virtually quadrate in shape, with lateral margins straight and parallel and anterior/posterior margins virtually straight and parallel. Lateral margins with a narrow rim. Meso- and metathoracic nota difficult to observe through fractures. **LEGS:** Fore and midlegs completely preserved (hind legs with tarsi lost at surface of amber). Forelegs raptorial, projected forward; coxae of all legs long, lengths approximately 0.5× length of respective femur, coxae extended posterior to basal attachment, femora apparently held anterolaterally. Fore and midfemora of equal length, hind femur slightly longer (1.1 times length of fore/mid femora). Forefemur slightly thicker than other femora (1.2 times width of midfemur in greatest thickness); ventral surface of forefemur flat with patch of about 70 fine, short, stiff hairs; ventromedial edge of femur with row of six fine, stiff, clear, spiculelike hairs (twice the thickness and length of the fine, ventral hairs), pointed ventrad; dorsomedial to this row is a row of about 10 finer, stiff hairs that are pointed anteroventrally; ventrolaterally is a row of three straight, fine, long bristles, about same length

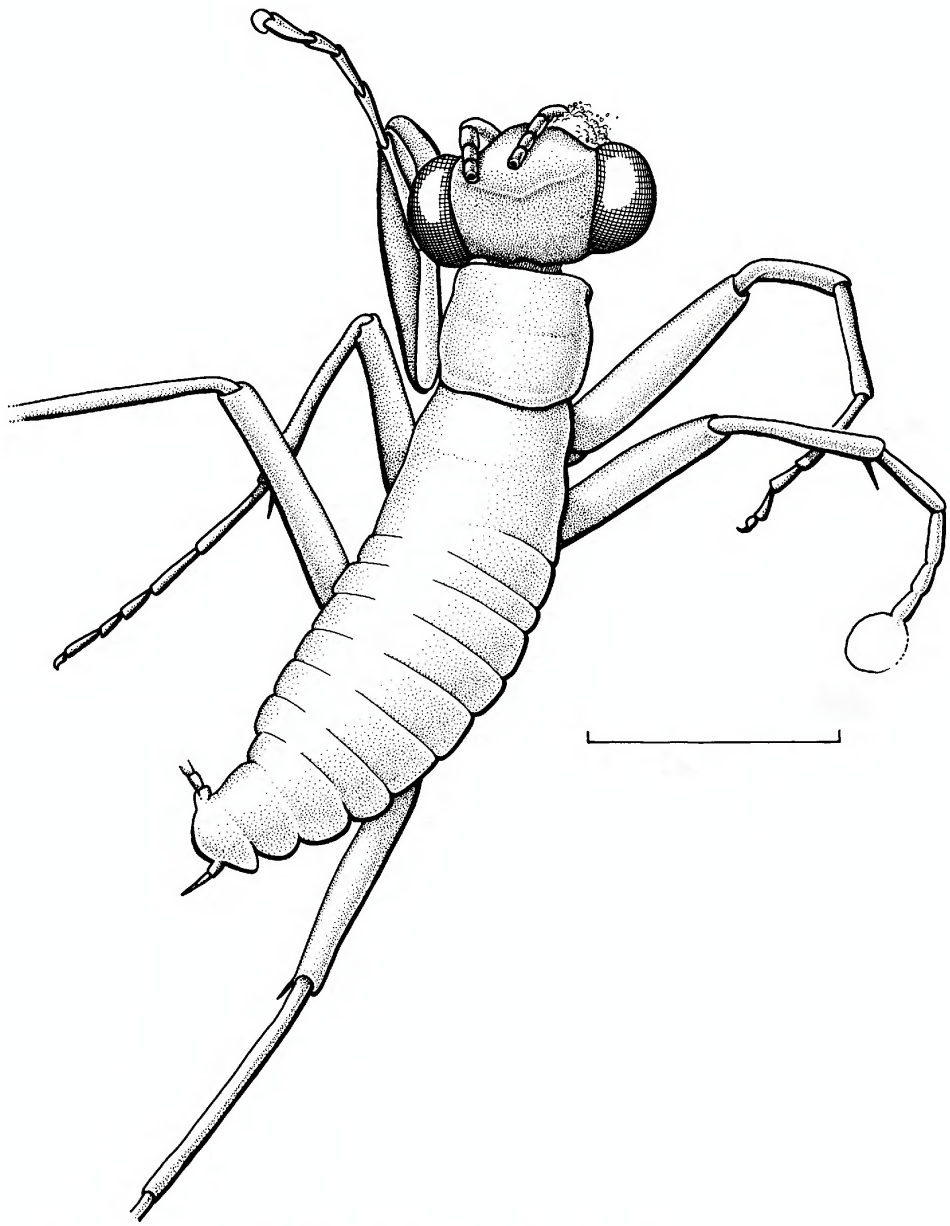

Fig. 2. Dorsal habitus of complete specimen. Scale = 1.0 mm.

as ventromedial ones. Foretibia slightly curved, 0.7 times length of femur; ventral surface flat, bordered mesally and laterally by row of stiff, fine bristles pointed anteroventrally: eight bristles in mesal row, six in lateral row, bristles evenly decreased in size proximad. Apex of foretibia with sharp, curved spur on mesal edge, spur has slight grooves in it; lateral edge with a thinner, shorter, horn-shaped spur. Five tarsal segments on each leg excluding pretarsus (hind tarsi were lost), ventral surface of each tarsomere with shallow groove; ventroapical corners of tarsomeres slightly projected into pair of blunt points. Relative lengths of leg segments (tibia: tarsomere 1 [basitarsus]: t2 : t3 : t4 : t5): for foreleg 5.2 : 4.5 : 2.5 : 2 : 1 : 2; for midleg 7.5 : 3 : 2.2 : 1.5 : 1: 2. Midtibia with pair of ventroapical spurs, mesal spur about 0.5 times length and thick-

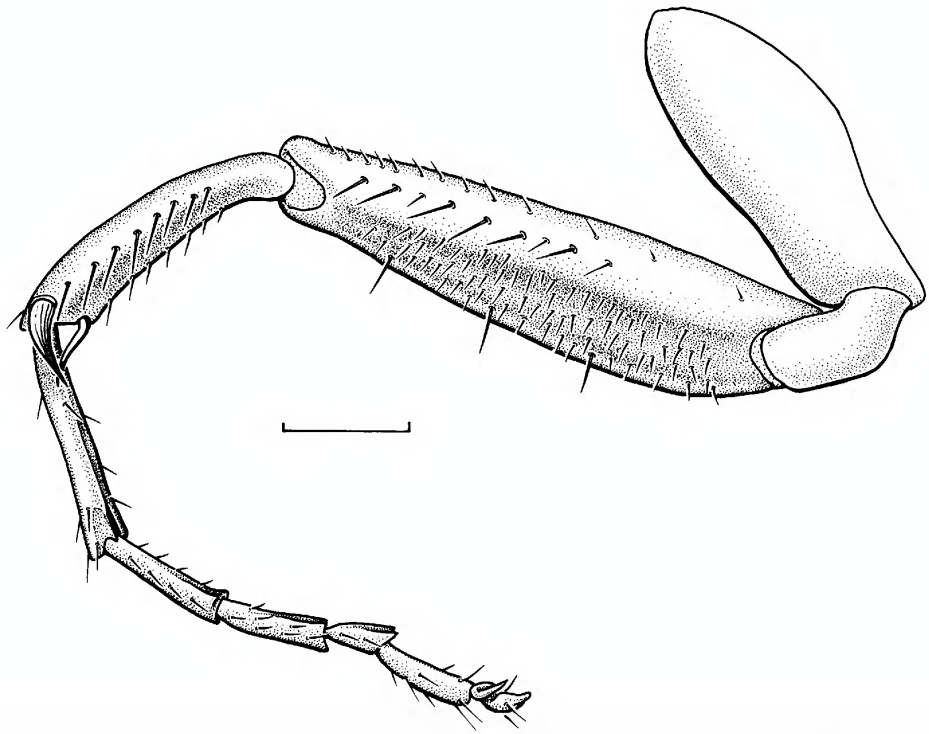

Fig. 3. Right foreleg of *Jersimantis luzzii,* ventromesal view. Scale = 0.2 mm.

ness of other. **ABDOMEN:** Moderately compressed dorsoventrally, with nine segments observable. Tapered apically. Cerci visible; left cercus not completely preserved, right cercus tapered to fine apex, with three segments visible. A milky coating covers much of the body, including virtually the entire ventral surface.

CONCLUSIONS

In lieu of wing venation characters, systematic placement of *Jersimantis* depends on the structure of the head, thorax, and legs. Fortunately, little allometric growth occurs in the proportions of thoracic and leg segments among juvenile instars and adults of mantises (Beier, 1968; Nickle, 1987). Thus, features of the juvenile fossil can be interpreted in the context of a taxonomy based on adults. If an adult mantis were to be discovered in New Jersey amber, the structure of the legs and proportions of the body would allow an identification as *Jersimantis* or not. It is highly doubtful that *Jersimantis* is one of the same taxa from the Russian Cretaceous, given the geographic and temporal separation (most of the taxa based on wings alone are 30–40 Ma older). *Jersimantis* is clearly distinct from the nymphs described in Siberian amber, as well as from *Cretomantis,* the nymph described from the Zaza Formation. It is unclear, actually, how *Cretomantis* was distinguished from taxa described as wings only, also from this formation. A taxonomy of fossils based on nymphs and some adult characters can lead to confusion. Given that body structures are more diagnostic for *groups within* mantises, it would be preferable to base a taxonomy on these and not venational characters, even if they are derived from nymphs.

The morphology of *Jersimantis* is indeed plesiomorphic. The nearly square pronotum is a feature occurring in the primitive family Chaeteessidae, although some living taxa have pronota with a length two to three times the width (e.g., the Australian *Cliomantis* and *Paraoxypilus*). Most mantises, though, have a pronotum that is at least three and up to ten times longer than wide. The presence of well-developed tibial spurs in *Jersimantis* is

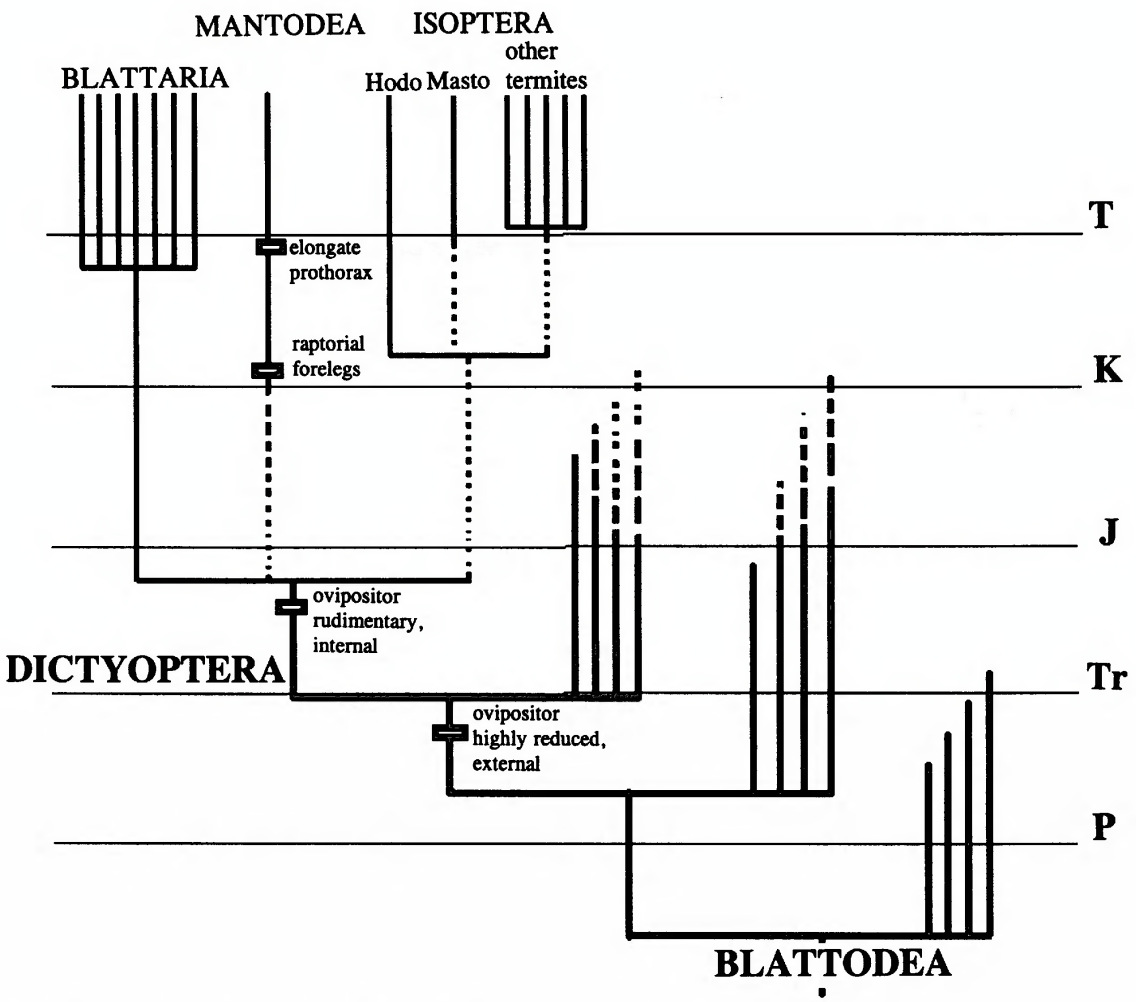

Fig. 4. Cladogram of dictyopteran orders on a geological scale, showing hypothesized relationship of early blattoids to the Dictyoptera.

probably plesiomorphic even compared to the Chaeteessidae, which have lost them. The square pronotum in combination with the primitive foreleg and tibial spines indicates the definitively primitive nature of *Jersimantis*. In particular, the forefemur is barely thicker than the other femora, and the forefemoral spines are sparse and very fine, not stout or even tubercular; again, much like the Chaeteessidae. *Jersimantis* appears most similar to *Chaeteessites minutissimus* Gratschev and Zherikhin, from the Santonian amber of Taymyr, Siberia. The lack of ocelli in *Jersimantis* is highly autapomorphic.

Although placement of the fossil in the Chaeteessidae is uncertain (indeed, monophyly of the Chaeteessidae has been questioned [e.g., Gratschev and Zherikhin, 1994]), the fossil is entirely consistent with a hypothesis of a Mesozoic origin of the Mantodea. In fact, the fossil record of the Mantodea parallels that of the Isoptera. Chaeteessid and chaeteessid-like mantis fossils, *the most primitive known forms, are the sole known representatives in the Cretaceous,* like the hodotermitid (and probably mastotermitid) termites. Moreover, chaeteessids and at least mastotermitids remain globally widespread through the Tertiary, becoming relict in the late Tertiary.

REFERENCES

Balderson, J.
1991. Mantodea. *In* The insects of Australia 1: 348–356. Melbourne: CSIRO.

Beier, M.
1968. Mantodea (Fangheuschrecken). Handb. Zool. 4(2) 2/12: 47 pp.

Boudreaux, H. B.
1979. Arthropod phylogeny with special reference to insects. New York: Wiley.

Carpenter, F. M.
1992. Treatise on invertebrate paleontology, Part R, Arthropoda 4. Vols. 3 & 4: superclass Hexapoda. Lawrence, KS: Univ. Kansas and Geol. Soc. America.

DeSalle, R., J. Gatesy, W. Wheeler, and D. Grimaldi
1992. DNA sequences from a fossil termite in Oligo-Miocene amber and their phylogenetic implications. Science 257: 1933–1936.

Emerson, A. E.
1967. Cretaceous insects from Labrador. 3. A new genus and species of termite (Isoptera: Hodotermitidae). Psyche 74: 276–289.

Grassé, P. P.
1949. Termites, Isoptères. Traité de Zoologie 9: 408–544.

Gratschev, V. G., and V. V. Zherikhin
1994. New fossil mantids (Insecta, Mantida [sic]). Paleontol. J. 27: 148–165.

Grimaldi, D.
1996. Amber: Window to the past. New York: Abrams/Am. Mus. Nat. Hist.

Grimaldi, D. A., C. W. Beck, and J. J. Boon
1989. Occurrence, chemical characteristics, and paleontology of the fossil resins from New Jersey. Am. Mus. Novitates 2948: 28 pp.

Hasiotis, S. T., and R. F. Dubiel
1993. Continental trace fossils of the Upper Triassic Chinle Formation, Petrified Forest National Park, Arizona. *In* S. G. Lucas and M. Morales (eds.), The Nonmarine Triassic, pp. 175–178. New Mexico Mus. Nat. Hist. Sci. Bull. 3.
1995. Termite (Insecta: Isoptera) nest ichnofossils from the Upper Triassic Chinle Formation, Petrified Forest National Park, Arizona. Ichnos 4: 119–130.

Hennig, W.
1969. Die Stammesgeschichte der Insekten. Hrsg. von der Senckenbergischen Naturforschenden Gesellschaft zu Frankfurt am Main. Frankfurt am Main, Kramer. Senckenb. Buch 49: 1–436.
1981. Insect phylogeny [translation and edited by A. C. Pont, with revisionary notes by D. Schlee]. New York: Wiley.

Jarzembowski, E. A.
1981. An early Cretaceous termite from southern England (Isoptera: Hodotermitidae). Syst. Entomol. 6: 91–96.
1994. Fossil cockroaches or pinnule insects? Proc. Geol. Assoc. 105: 305–311.

Kambhampati, S.
1995. A phylogeny of cockroaches and related insects based on DNA sequence of mitochondrial ribosomal RNA genes. Proc. Natl. Acad. Sci. 92: 2017–2020.

Krishna, K.
1990. Isoptera, *In* D. Grimaldi (ed.), Insects from the Santana Formation, Lower Cretaceous, of Brazil. Bull. Am. Mus. Nat. Hist. 195: 76–81.

Kristensen, N. P.
1975. The phylogeny of hexapod "orders." A critical review of recent accounts. Z. Zool. Syst. Evolution Porsch 13: 1–44.
1995. Forty years' insect phylogenetic systematics. Zool. Beitr. 36: 83–124.

Kukalova-Peck, J.
1991. Fossil history and the evolution of hexapod structures. *In* The Insects of Australia 1: 141–179. Melbourne: CSIRO.

Lacasa-Ruiz, A., and X. Martinez-Delclos
1986. *Meiatermes:* nuevo genero fosil de insecto Isoptera (Hodotermitidae) de las calizas Neocomienses des Montsec (Provincia de Lerida, Espana). Lleida: Inst. Est. Ilerdencs.

Laurentiaux, D.
1951. Le problème des blattes paléozoiques a ovipositeur externe. Ann. Paleontol. 37: 187–194.

Nel, A., and J. C. Paicheler
1993. Les Isoptera fossiles. Etat actuel des connaissances, implications paléoécologiques et paléoclimatiques. Cah. Paléont., CNRS: 102–179.

Nel, A., and R. Roy
1996. Revision of the fossil "mantid" and "ephemerid" species described by Piton from the Palaeocene of Menat (France) (Mantodea: Chaeteessidae, Mantidae; Ensifera: Tettigonioidea). Eur. J. Entomol. 93: 220–234.

Nel, R. J.
1929. Studies on the development of the genitalia and the genital ducts in insects. I. Female of Orthoptera and Dermaptera. J. Microsc. Sci. 73: 25–85.

Nickle, D. A.
1987. Order Mantodea, *In* F. Stehr (ed.), Immature insects: 140–142. Dubuque, Iowa: Kendall/Hunt.
Pike, E. M.
1995. Amber taphonomy and the Grassy Lake, Alberta, amber fauna. Ph.D. diss., Univ. of Calgary.
Poinar, G. O., Jr.
1992. Life in amber. Palo Alto: Stanford Univ. Press.
Schlee, D.
1990. Das Bernstein-Kabinett. Stuttgarter Beitr. Natkd. (C) 28: 100 pp.
Schlüter, T.
1989. Neue Daten über harzkonservierte Arthropoden aus dem Cenomanium NW-Frankreichs. Documenta Naturae 56: 59–70.
Thorne, B. L., and J. M. Carpenter
1992. Phylogeny of the Dictyoptera. Syst. Entomol. 17: 253–268.
Vishniakova, V. H.
1968. Mesozoic blattids with external ovipositor, and peculiarities of their reproduction. *In* B. B. Rohdendorf (ed.), Jurassic insects of Karatau, pp. 55–86. Moscow: Akademie Nauk SSSR [in Russian].

Recent issues of the *Novitates* may be purchased from the Museum. Lists of back issues of the *Novitates* and *Bulletin* published during the last five years are available at World Wide Web site http://nimidi.amnh.org. Or address mail orders to: American Museum of Natural History Library, Department D, Central Park West at 79th St., New York, N.Y. 10024. TEL: (212) 769-5545. FAX: (212) 769-5009. E-MAIL: scipubs@amnh.org

♾ This paper meets the requirements of ANSI/NISO Z39.48-1992 (Permanence of Paper).